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The effect of wave action on the shell morphology of *Littorina unifasciata* Gray

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Abstract

The aperture length/spire height ratio was determined for populations of *Littorina unifasciata* up a vertical slope in an exposed and a projected site. It was found that a significantly larger ratio occurred in the lower levels of the exposed habitat than on all the levels in the sheltered site. There was no difference between levels at the two sites.

It is argued that the change in mean phenotype of this continuously variable trait may be the result of natural selection produced by varying degrees of wave action and desiccation.

Introduction

The common gastropod mollusc *Lottorina unifasciata* Gray is found on the rocky shores of Western Australia as far north as North-West Cape (Wilson and Gillett 1979) ranging from the supra-littoral down to the upper tidal zone. Of all the grazing molluscs present on the vertical intertidal rock walls of Rottnest Island, it is found uppermost in the vertical range (Black *et al.* 1979). Living in the intertidal zone subjects the fauna to a variety of environmental factors which result in gastropods displaying a wide range of morphological adaptations.

Major environmental factors thought to be responsible for shell variations in gastropods are wave action, prolonged submersion, high temperatures, extreme salinity, desiccation (Struhsaker 1968 Newkirk and Doyle 1975) and predation by animals such as crabs (Hughes and Elner 1979). The shell shape in the Western European Dog-Whelk, *Nucellus lapullus* has long been known to vary with exposure, animals with short squat shells being found on exposed headlands whilst those with elevated and sharply pointed spikes are restricted to sheltered inlets (Kitching *et al.* 1966, Berry and Crothers 1968). The shell-shape ratio (length of aperature: height of spire) has been shown to be directly related to an exposure scale devised by Ballantine (1961) in southern and Western parts of Europe (Crothers, 1974, 1975a, 1975b, 1977, 1981; Crothers and Cowell 1979). However, populations in certain parts are quite different (Crothers 1981), and even though in all these places the shells are more elongated than would have been expected from the regression it cannot be assumed that the correlation is universal in this particular species.

The present preliminary investigation was intended to establish whether shell-shape ratio in populations of *L. unifasciata* is in any way related to the degree of wave action (exposure) on vertical rocky shores.

Materials and methods

The two study sites from which the populations were measured were on exposed and a protected section of rocky shore at Point Peron, Western Australia. The different degree to which the two rock faces are subjected to wave action were determined by counting the approximate splash height reached by each of 150 waves during a high tide period.* The two sites are opposite sides of a vertical limestone wall: the exposed side faced the open sea while the protected side was situated in a protected cove.

Samples were taken from each site at the low water mark, which was the lowest level the snail was found, the upper limit of the splash zone and an area in the middle of the two limits. The range from lower to upper was approximately one metre. Such a small scale was possible because patterns of tidal influence occur on a scale of centimetres on vertical shores characteristic of coastal limestone of Western Australia. Also littorines shift their position little after grazing excursions relative to tidal conditions. (Black *et al.* 1979). All three levels of both sites were sampled at the same time on three occasions, 25 April, 11 May and 4 June 1981. During the first two collections 70 shells were measured from each of the six areas while 140 were collected on the last date.

The maximum height of the spire (H) and length of the aperture (L) was measured to the nearest 0.1 mm for each snail using vernier calipers (Fig. 1). The results were expressed as the length/height ratio in order to eliminate the variation in size due to differing ages of the individual specimens. *L. unifasciata* has a planktonic larval phase. The juveniles settle on the lower shore levels after metamorphosis and migrate upwards as they grow. The ratio of aperture length/spire height varies with size. Therefore, to eliminate differences in the size frequency characteristics between exposed and protected shores being caused by differential settlement or size selective mortality only individuals with a spire height above 7 mm were measured.

*This method of measuring wave action does not measure the force exerted by the waves (a simple technique is not available) nor is it an objective method. A more quantitive technique was attempted using Calcium sulphate clods (Doty 1971) but these were quickly destroyed on the exposed site. There was also no way of devising an exposure scale such as that of Ballantine (1961) as little floral or faunal zonation existed along the vertical slope.

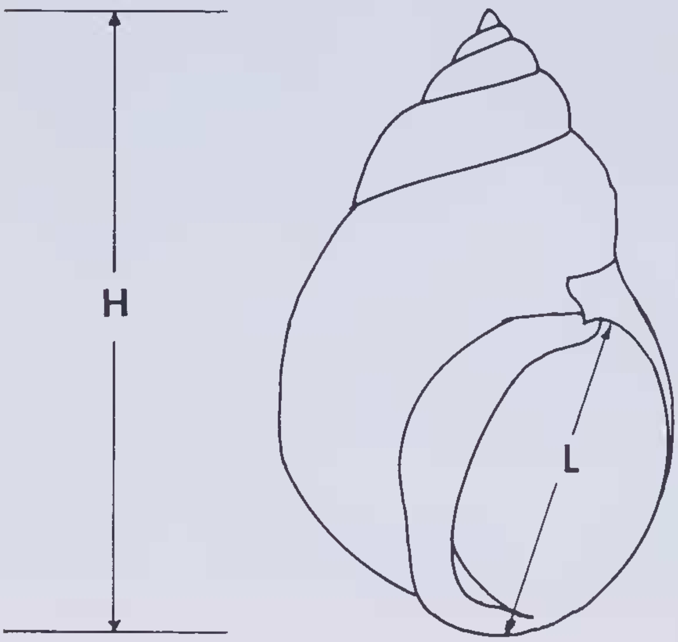

Figure 1.—Aperture length (L)/spire height (H) measurement of *L. unifasciata*.

The six populations were tested for significant difference using the two-tailed "Z" statistic. It should be noted that any differences observed were due to shape and not size as the aperture length and spire height values were highly correlated for both exposed and protected sites (r=0.87 and 0.90 respectively).

Results

The results of Table 1 indicate that the degree of splash by wave action differs between the exposed and protected sites and along the vertical gradient.

Table 1

Average number of times the zones are covered or splashed (min^{-1}) at high tide.

Site	Upper level	Middle level	Lower level	Mean
Protected....................	0.1	0.5	5.0	1.9
Exposed......................	1.0	5.3	8.6	5.0

Each determination is the mean of 150 measurements

At the exposed site the whole population of *L. unifasciata* has a significantly larger ratio than the population sampled at the protected site (p<0.001). It can also be seen that at both sites there is no significant difference in ratio between any of the three vertical levels (Tables 2 and 3). The snails situated at the sheltered site have a slightly smaller but significantly different ratio than the snails from two lower positions at the exposed site (p<0.05).

Table 2

Aperture length/spire height ratio of *L. unifasciata* populations collected from three vertical levels at a protected and an exposed site at Point Peron.

Site	Upper level	Middle level	Lower level	Mean
Protected....................	(A) 0.655 ± 0.003	(B) 0.657 ± 0.003	(C) 0.650 ± 0.003	(G) 0.654 ± 0.002
Exposed......................	(D) 0.670 ± 0.003	(E) 0.679 ± 0.003	(F) 0.679 ± 0.003	(H) 0.676 ± 0.002

Table 3

"Z" Scores and levels of significance of *L. unifasciata* population comparisons on the three levels at the two sites. The operator error factor was 0.2 mm for aperture length and 0.1 mm for spire height calculated to Xy ± 0.008

	B	C	D	E	F	H
A....	+3.02 ns	1.28 ns	-0.25 ns	-2.46 p<0.05	-2.54 p<0.05	—
B....		+1.76 ns	+0.24 ns	-1.97 p<0.05	-1.99 p>0.05	—
C....			-1.49 ns	-3.69 p<00.1	-3.81 p<0.001	—
D....				+1.20 ns	+1.23 ns	—
E....					0.00 ns	—
F....						—
G....						-3.48 p<0.001

ns = not significant

Figure 2 shows that in all six populations the ratio had a continuous distribution and most likely it is polygenic. The medians of the sheltered situations were skewed towards the lower ratios compared with those from the exposed site.

Discussion

As with many intertidal gastropods throughout the world (Stephenson and Stephenson 1954, Berry and Crothers 1968, James 1968, Kitching *et al.* 1968, Struhsaker 1968, Vermeij 1973, Newkirk and Doyle 1975) there appears to be a change in shell shape correlated with habitat in the Australian snail, *L. unifasciata.*

The selection pressures acting on the parameters measured seem to be different in the two extreme habitats, and greater between sites than between levels. On the exposed rocks where there is a great deal of wave action, there must be selection for morphological features which decrease the turbulence of water flowing over the shell. There must also be selection for increased area of contact with the substrate. This can be achieved by increasing the size of the aperture relative to the height of the spire.

Such a morphological change is evident when one compares the exposed populations at Point Peron, subject to heavy wave action, with the more sheltered populations. The populations on the lower levels at the exposed site, particularly are subject to more intensive wave action.

Although on protected shores there is not so much splashing as on exposed shores, Black *et al.* (1979) clearly showed a gradient in desiccation stress on vertical rocky shores of Rottnest Island. The result is selection to reduce the size of the aperture relative to the height of the shell. However, there is no significant difference in shell shape between the levels at the sheltered site. Thus although desiccation may be a selection pressure it does not seem to be as important as wave action but it appears to eliminate the possibility of predators such as crabs being a method of selection as these are purported to be more abundant on protected regions (Crothers 1968, 1970).

Irrespective of the relative importance of the selection pressures, it is not obvious whether the environmental influence is developmental or genetical.

However, variation of all populations shows a continuous distribution and the changes in shell morphology are by a directional shifting of the median left or right (Fig. 2) suggesting a genetical contribution.

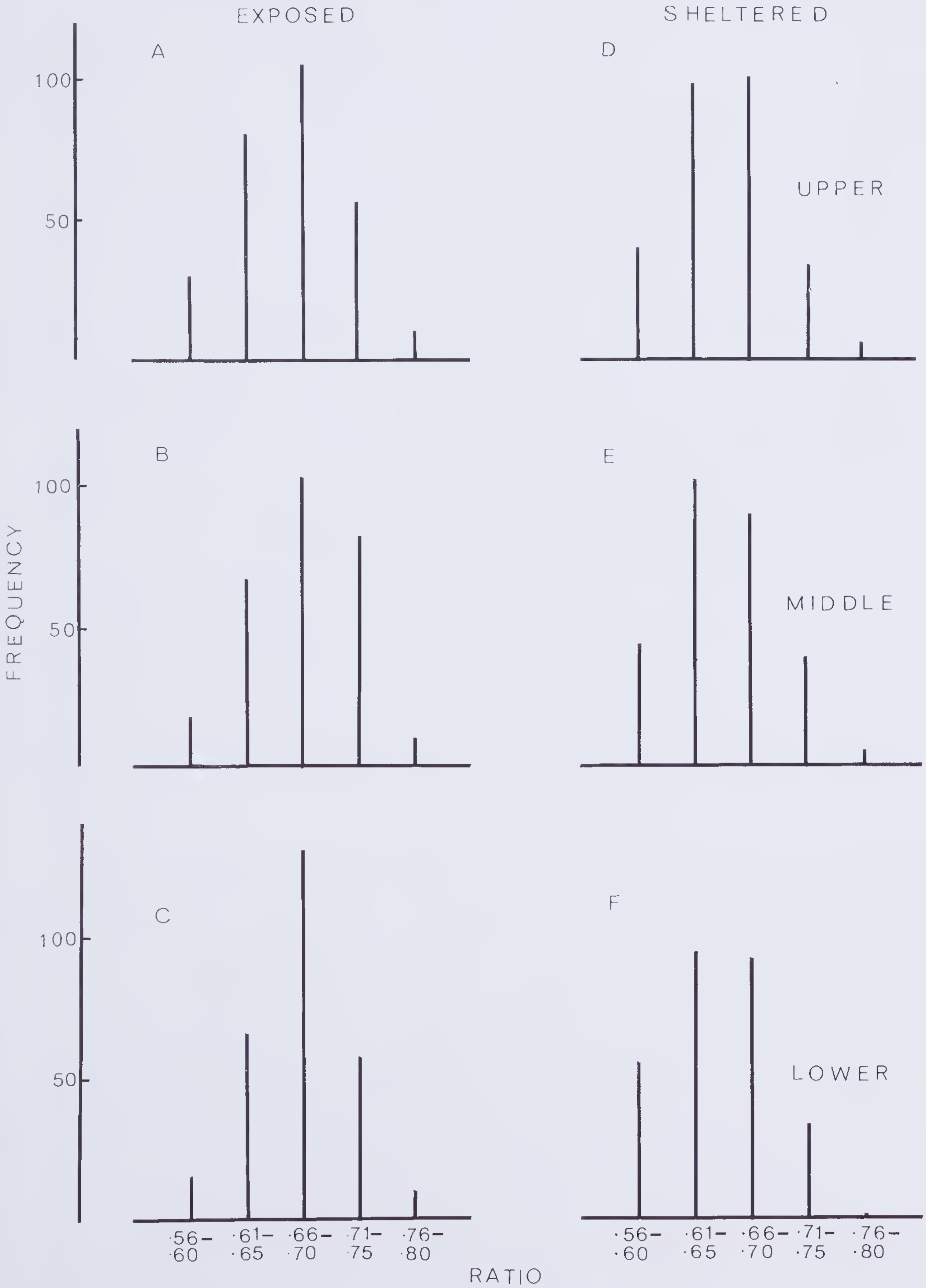

Figure 2.—Frequency of aperture length/spire height ratio classes of *L. unifasciata*.

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